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Understanding intentions from actions: direct perception, inference, and the roles of mirror and mentalizing systems

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Abstract

This review asks whether observers can obtain information about others' intentions from observation of their actions; and if so, whether this process is performed using direct perceptual or inferential processes (prominent examples of each being the intention understanding theory of mirror neuron function, and mentalizing accounts of intention understanding, respectively). I propose four conditions that should be fulfilled in order to support a direct perception account, and suggest that only two of these conditions are supported by the existing data. I then propose and review three further sources of evidence which have the potential to inform this debate, concluding that the data do not support the direct perception account. In particular, mirror neurons may be involved in lower-level processes of action perception, but there is no evidence to support their involvement in the type of higher-level intention understanding that is proposed by the direct perception account.

Keywords: mental states; intentionality; intention understanding; action observation; action understanding; mirror neurons; kinematics; mentalizing; direct perception; inference

1. Introduction

The overarching question of this special issue is how humans acquire information about other people's mental states. In this review I focus on one particular type of mental state: that of having an intention, i.e. a motive to perform an action in order to produce an effect; and I discuss the processes by which humans can acquire information about others' intentions, i.e. identify *why* an action was performed, from the observation of their actions.

The link between action observation and intention understanding has garnered particular interest over the last two decades due to the discovery of 'mirror' neurons in the macaque (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) and subsequently the human (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) brain. These neurons have been found primarily in motor areas of the macaque brain (although the human data suggest that they may be considerably more widespread) including premotor, primary motor, and parietal cortex (di Pellegrino et al., 1992; Fogassi et al., 2005; Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009). The defining characteristic of a mirror neuron is that it fires both when performing an action, and when passively perceiving the same, or a related, action performed either by a conspecific or an experimenter (the perceived action can be presented in either the auditory or visual modality: Cook, 2012; Kohler et al., 2002; but for conciseness, this review will focus on vision as the modality in which the majority of research has been performed). Thus, mirror neurons appear to match the observation of another's action with the motor program that would be required for the observer to produce that action themselves. This characteristic has led to speculation that mirror neurons underlie the ability to understand others' intentions by observing their actions. For example, it has been claimed that mirror neurons allow us to "… understand the actions of others by means of our own 'motor knowledge': this knowledge enables us immediately to attribute an intentional meaning to the movements of others" (Rizzolatti & Sinigaglia, 2007, p. 205). The term 'intention' has been used in the mirror neuron literature to refer both to the immediate outcome of an action, and to the higher-level motivation that produced the action. This review focuses on the latter definition because it is more clearly related to the mental state of having an intention. In addition, this definition has excited the most interest precisely because it suggests that mirror neurons provide a mechanism for identifying an actor's underlying intention. However, the evidence either for or against this claim is relatively sparse (Cook, Bird, Catmur, Press, & Heyes, 2014). It is therefore important to establish: whether we can indeed acquire information about others' intentions from observation of their actions; whether this process is performed by mirror neurons, and if not, what are the alternative candidate processes for acquiring information about intentions; and which of these processes is best supported by the existing data.

In section 2 I review evidence for whether it is possible to acquire information about intentions from the observation of others' actions: is information about intentions indeed present in performed actions, and if so, do observers make use of this information? The third section asks how observers can acquire this information, and sets out the competing possibilities, with reference to the distinction between direct perception and inferential processes described by Michael and de Bruin (this issue). I discuss what would constitute evidence for one of these processes over another, and review the current research in this area. I conclude that there is insufficient evidence to support the involvement of mirror neurons in understanding others' intentions, and that the existing data are better explained by the involvement of inferential processes.

2. Can we acquire intentions from actions?

In order to acquire information about an actor's intentions from the observation of their actions, two conditions need to be fulfilled (see Ansuini, Cavallo, Bertone, & Becchio, 2014, for a more detailed discussion of this literature). First, there need to exist reliable perceptual differences between actions performed with different intentions; and second, observers must be able to detect and utilise these differences to make judgements about the actor's intentions.

2.1. Intentions modulate action kinematics

A substantial body of evidence indicates that an actor's intentions can indeed modulate the kinematics of their subsequent action. Importantly, the kinematics of reach-to-grasp actions are modulated even when actions are performed on the same object, but with different intentions. Thus Marteniuk and colleagues (1987) demonstrated differences in the kinematic profiles of actions when the actor's intention was to place an object carefully into a small container, versus into a large box (see Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006, for a similar result). Consistent with these results, Schuboe and colleagues (2008) showed kinematic differences between actions towards a bottle depending on whether the intention was to pour or to place the bottle; and a comprehensive set of studies from Becchio and colleagues demonstrated differences in kinematics between cooperative and competitive actions, between social and non-social actions, and between individual and communicative actions (Becchio, Sartori, Bulgheroni, & Castiello, 2008; Georgiou, Becchio, Glover, & Castiello, 2007; Sartori, Becchio, Bara, & Castiello, 2009). Most recently, Naish and colleagues (2013) demonstrated systematic differences between the kinematic profile of reach-to-grasp movements depending on whether the intention of the movement was to place an object or to bring it to the mouth. Thus it appears that actions performed with different intentions do result in reliable kinematic, and thus presumably perceptual, differences.

2.2. Do observers use action kinematics to acquire intention information?

Whether observers are able to use these kinematic differences to make judgements about an actor's intentions is less clear-cut. Work from Becchio and colleagues indicated that observers can use kinematic information to judge whether actions are performed in a competitive or cooperative context (Sartori, Becchio, & Castiello, 2011); and that observers can extract and use this kinematic information to make such judgements even from relatively degraded point-light displays (Manera, Becchio, Cavallo, Sartori, & Castiello, 2011). Similar results from Stapel and colleagues (2012) indicated that observers use kinematic information to determine whether an actor intends to continue walking or to crawl in order to reach a target object. In contrast, Naish et al. (2013) demonstrated that observers were not able to use kinematic information to decide whether an actor was performing a reaching movement in order to place an object, or in order to eat it. This inability to acquire intention information from kinematics is perhaps surprising since there were reliable differences between the kinematic profiles of these two types of action (see section 2.1). However, Naish et al. did not test whether participants were able to *detect* a difference between the two profiles (for example, by using a delayed match to sample task). Such a task would establish whether the differences between the two kinematic profiles were not perceived by the observers, or whether these differences were perceived but instead observers were unable to label or identify the profiles as 'reach-to-place' versus 'reach-to-eat'.

In conclusion, it appears that in most cases observers are able to use kinematic information to acquire information about actors' intentions; but it will be important for future work to establish whether failures to use such information are due to an inability to detect kinematic differences, or to identify the intention associated with the kinematic profile. Another important question for future research is whether kinematic information is useful when judging intentions from richer stimuli in more ecologically valid settings.

3. How do we acquire intentions from actions?

In cases where observers are able to acquire intention information from action kinematics, how does this process occur? Michael and de Bruin (this issue) set out two competing possibilities: intention information may be acquired from action kinematics via 'direct' perception, or via inferential processes. Direct perception accounts suggest that perception of others (in this case of their action kinematics) results in 'direct' awareness of their mental states (in this case of their intentions). The suggestion by Rizzolatti and Sinigaglia (2007; see also Rizzolatti & Fogassi, 2014) that mirror neuron responses allow us "immediately to attribute an intentional meaning to the movements of others" fits within a direct perception framework if 'intentional' refers to the actor's underlying motivation for performing the observed movement. (If, instead, 'intentional' refers to the outcome of the actor's movement, it could be argued that mirror neuron responses are not an example of direct perception because they do not provide any information about the underlying mental state of the actor. This may well be the case, but as stated above, the word 'intention' is used in the mirror neuron literature to refer to something more akin to mental states than to identification of an action outcome, and my interpretation follows this more common usage of the term 'intention'.) In contrast, inferential accounts suggest that perception of action kinematics is followed by the recruitment of other cognitive or inferential processes that lead to awareness of the other's intentions.

It is clear from this description that definitions of perception and of inference are crucial to this debate; however, as Michael and de Bruin note, there is a risk of reducing this discussion to a mere terminological argument. In addition, these definitions are addressed in greater detail elsewhere in this special issue. Therefore, rather than focus on definitions, I address this question from two alternative angles, asking first, whether a mirror response can be considered to constitute intention understanding; and second, what kinds of evidence would support a direct perception over an inferential account of intention understanding, where 'direct perception' encompasses, but is not limited to, the 'immediate' attribution of intention described in the quote above. I then review the evidence for these two accounts.

3.1. Do mirror neuron responses *constitute* intention understanding?

Proponents of the intention understanding theory of mirror neuron function have suggested that the presence of mirror responses (activation of same motor program as that used by the actor) is, itself, a kind of intention understanding: that activation of a motor program by the sight of another's action corresponds to understanding of their intentions. As we have discussed elsewhere (Cook et al., 2014) this claim is potentially circular: it is not possible to ask whether mirror neuron responses are the basis of intention understanding if such responses are defined as constituting intention understanding.

However, if mirror responses do not *per se* constitute intention understanding, it may still be useful to ask under what conditions such responses *could* correspond to understanding of the other's intentions. To recap: a mirror response indicates that the same motor program is active in the observer as in the actor. In order for this to qualify as a direct understanding of the other's intentions, I suggest that at least four conditions need to be fulfilled: 1) the sight of an action must activate only one, matching, motor program in the observer; 2) this motor program must have a one-to-one mapping with the observer's own intention; 3) this mapping from motor program to intention must be the same in the observer as in the actor; and 4) upon activation of the motor program, the associated intention must be automatically activated, without the involvement of any higher-level inferential processes.

The reasoning behind these conditions is as follows: 1) if more than one motor program (or a non-matching motor program) is activated in the observer, then multiple intentions (or the 'wrong' intention) could be attributed to the actor; 2) and 3) if the observer's motor program does not correspond to one and the same intention as that of the actor's motor program, again the 'wrong' intention could be attributed; and finally, without condition 4), mirror responses may *contribute* to intention understanding but cannot *correspond* to intention understanding (unless activation of a motor program constitutes intention understanding, with the associated circularity this claim implies). It should also be noted that a full account of how mirror responses contribute to intention understanding must show how they contribute over and above purely perceptual processes (e.g. vision).

Section 2.1 suggests that conditions 2 and 3 may be fulfilled, because – at least within the limits of the types of action used in these studies – actions performed with different intentions produce patterns of kinematics which are distinct for different actions and consistent across actors. In contrast, the evidence for condition 1 has been scrutinised recently (Cook & Bird, 2013): macaque 'mirror' neuron responses indicate that the observation of an action does not always activate a matching motor program in the observer. In fact, the majority of 'mirror' neurons respond to the observation and performance of similar, but not necessarily exactly the same, actions. Without strict congruency between the motor programs of actor and observer, the claim that mirror responses are sufficient for intention understanding becomes precarious. Finally, condition 4 has not, to my knowledge, been investigated directly, although related questions are addressed in sections 3.3-3.5.

In conclusion: to establish whether mirror responses are involved in intention understanding, future research needs to establish whether action observation consistently leads to activation of a *matching* motor program in the observer; whether activation of a motor program consistently and inevitably leads to the activation of the associated intention; and whether this results in a greater ability to understand an actor's intentions than would be possible with vision alone. Without such evidence, it would be premature to conclude that mirror responses constitute direct attribution of others' intentions. Therefore section 3.2 asks what other types of evidence could support a direct perception over an inferential account of intention understanding.

3.2. Types of evidence

One source of evidence relates to the timecourse of intention understanding. Compared to direct perception accounts, inferential accounts posit an additional processing stage between perception and awareness of intentions; thus it might be reasonable to suppose that direct perception accounts

predict faster processing of others' intentions than inferential accounts. However, it is certainly not easy to define how early a process has to occur for it to be considered non-inferential.

Another interesting approach is to consider the role of attention in perceptual processing. Attention binds together features (e.g. line orientation, colour) which are processed separately at earlier stages of perception (Treisman & Gelade, 1980). Therefore, if the processing of others' intentions can occur without attention, this might be evidence that such processing is occurring pre-attentively, i.e. without additional inferential or cognitive demands.

The quality of perceptual stimulus required in order for intention inferences to be drawn is a source of evidence whose support for either account is equivocal. It is clear from section 2.2 that intention information can be acquired from relatively impoverished stimuli, including point light displays of actions, in which the only distinguishing feature between alternative stimuli is the action kinematics. On the one hand, this appears to support a direct perception account: intention information can be acquired without the rich contextual information which might support inferential reasoning. On the other hand, the absence of contextual information might instead encourage the use of inferential processes to 'fill in' missing information. It is not clear, therefore, whether the ability of observers to acquire intentions from impoverished stimuli would be strong evidence for either account.

A final potential source of evidence is to consider the brain networks involved in intention understanding. Put simplistically, if intention understanding recruits low-level perceptual or motor areas (including, for the sake of argument, mirror neuron areas; but see section 3.1) this would better support a direct perception account, whereas recruitment of executive function areas such as those involved in theory of mind or mentalizing might support an inferential account. Problems of reverse inference aside, is it possible to characterise the brain areas involved in the acquisition of intention information from others' actions? The difficulty here is that neural responses alone do not demonstrate that an intention has been identified. For instance, differences in the neural responses to two different actions may reflect perceptual processing of the two different kinematic profiles, rather than identification of the actor's differing intentions. Therefore brain imaging techniques need to be used in combination with carefully designed behavioural tasks that measure intention understanding, and which distinguish intention understanding from action perception.

The following behavioural definitions (see also Spunt, Falk, & Lieberman, 2010; Spunt, Satpute, & Lieberman, 2011; Spunt & Lieberman, 2012) are an attempt to operationalise this distinction. Action perception comprises processes that allow the observer to distinguish one action from another, to identify *what* is being done, and *how* an action is being performed. Intention understanding comprises processes that allow the observer to identify *why* an action is being performed, which may involve identification of the actor's immediate intention (to grasp a cup) or their higher-level intention based on contextual information (to drink versus to tidy up; Iacoboni et al., 2005). These definitions highlight the need to design behavioural tasks that measure these different abilities, to be used both in brain imaging studies and along with causal techniques such as brain stimulation, in order to demonstrate whether particular brain areas are required for intention understanding, rather than for perceptual processing of kinematic differences.

Overall, this analysis suggests that if the process of identifying another's intention from their actions takes place quickly, without attention, and involves mostly low-level perceptual or motor brain networks, it would satisfy the requirements of a direct perception account. If in contrast

identification of intention takes place more slowly, requires attention, and involves higher-level mentalizing networks, this would support an inferential account.

3.3. Timecourse of intention understanding

Two alternative approaches have been used to establish how quickly the process of identifying another's intention occurs. The first is to measure response times to identify another's intention; the second is to identify the timepoint at which neural responses to observed actions differ systematically as a function of the actor's intentions.

A typical choice response time for a perceptual discrimination task is around 250-300 ms (e.g. Mochizuki, Franca, Huang, & Rothwell, 2005; Neubert, Mars, Olivier, & Rushworth, 2011). In contrast, response times for intention identification tasks are considerably longer and also show a wide degree of variability: Ortigue and colleagues (2009) demonstrated that response times to identify the intention of an action (whether the actor intended to use an object or to move it) were around 600 ms (however, these relatively fast responses were accompanied by relatively low accuracy, and a similar task used by Avanzini and colleagues (2013) elicited response times of around 900 ms); whereas response times in Sartori et al. (2011)'s study were around 1200 ms, and those of Manera et al. (2011) around 1500 ms. In both of the latter studies, participants were asked to distinguish between cooperative and competitive intentions; it is possible that this is a more difficult distinction than that between using and moving an object, or that the two actions are perceptually more similar, making discrimination between the two more difficult. It should also be noted that the latter two studies used video stimuli and it was not specified from which timepoint the kinematics for the two intentions started to differ, which may also contribute to the longer response times. Although it is difficult to define exactly how fast a response should be to constitute evidence for direct perception, the range of response times reported across these experiments suggests that there is not a single, fast, path to intention identification.

The second approach to measuring the timecourse of intention identification does not require an overt behavioural response, thus removing those elements of the response time which relate to response key selection and purely motoric processes. For example, Ortigue et al. (2009) used electroencephalography to measure the timecourse of the neural response while participants were asked to identify an actor's intentions. They found that novel, compared with repeated, intentions, generated a different response at two timepoints, 60-130 ms and 330-400 ms after the onset of action information which discriminated between intentions. However, differences in neural response may reflect perceptual processing, rather than intention identification.

To the extent that a mirror response is considered by some authors to constitute intention understanding it may be worth reviewing data on the timecourse of mirror responses. A recent overview of mirror neuron response timecourse (Cavallo, Heyes, Becchio, Bird, & Catmur, 2014) and a more comprehensive review of the human data (Naish, Houston-Price, Bremner, & Holmes, 2014) both concluded that there is no evidence for mirror responses before 200 ms after the onset of an observed action. Although a latency of 200 ms would appear to be relatively fast, this should be compared with the latency of motor cortex responses during perceptual discrimination in response selection tasks: premotor-primary motor connections discriminate between different shaped cues as early as 75 ms (O'Shea, Sebastian, Boorman, Johansen-Berg, & Rushworth, 2007).

Thus, neural responses may differentiate between actors' intentions as early as 60 ms after the onset of discriminating information, but it is not clear whether such responses reflect anything more than the perceptual differences between novel and repeated intentions. Matching motor ('mirror') responses to others' actions are found after 200 ms, but whether such responses constitute intention understanding is an outstanding empirical question (section 3.1). Behavioural responses when explicitly instructed to identify actors' intentions are of variable and relatively long latency. These data do not provide consistent support for a fast, direct process for intention understanding.

3.4. The role of attention in intention understanding

Little previous work investigates whether intention understanding can occur pre-attentively. Given the lack of research into this question, and although section 3.1 casts doubt on whether activation of one's own motor program by the sight of another's action constitutes intention understanding, it may be useful to ask whether mirror responses occur under conditions of no, or limited, attention.

Recent data on imitative compatibility (the tendency to perform an action faster when observing the same action than a different action; Heyes, 2011; Stürmer, Aschersleben, & Prinz, 2000), a behavioural effect that is thought to index mirror neuron function (Catmur, Walsh, & Heyes, 2009; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Hogeveen et al., in press), supports the conclusion that mirror responses can occur with limited attention. Catmur (under review) used an imitative compatibility design to demonstrate that the mapping of an observed movement onto the motor program for that movement occurs under conditions of limited attention (however see Chong, Cunnington, Williams, & Mattingley, 2009, for an alternative finding); and Dainton, Catmur, and Marsh (in preparation) showed that attention affects spatial, but not imitative, compatibility.

Similar results come from neuroimaging data: both Chong and colleagues (2008) and Spunt and Lieberman (2013) demonstrated that responses to observed actions in most mirror neuron areas were not modulated by attentional demands. Interestingly, however, Spunt and Lieberman also included a task which asked participants to infer the actor's intentions. In contrast to the effects on mirror neuron areas, the neural response in mentalizing regions during this intention understanding task *was* modulated by attention.

Thus there is mixed evidence regarding whether mirror responses occur with limited attention. In addition, unless we accept the claim that mirror responses constitute intention understanding, this does not address the question of whether *intention understanding* occurs pre-attentively. The fact that manipulation of attention during an intention understanding task resulted in a reduction in response in mentalizing regions (Spunt & Lieberman, 2013) suggests that intention understanding may not occur pre-attentively; however, it will be important for future research to assess behavioural measures of intention understanding under conditions of limited attention.

3.5. Brain networks involved in intention understanding

The results above lead to the question of which brain networks respond when participants are asked to infer an actor's intentions. Some studies have demonstrated increased neural response in mirror neuron areas when inferring intentions from actions (e.g. Vingerhoets et al., 2010); however, others have found increased response in areas associated with mentalizing. For example, Brass and colleagues (2007) measured neural responses while participants observed unusual actions in

plausible or implausible contexts. Increased response was found in mentalizing but not in mirror neuron areas for implausible actions, suggesting that inferential, rather than mirroring, processes underlie intention understanding for implausible actions.

Further studies have delineated the involvement of both mirror and mentalizing brain areas when participants are asked to infer actors' intentions. The pattern of responses may depend to some extent on the type of actions used: irrational, implausible or unusual actions generally produce greater responses in mentalizing areas (Liepelt, Von Cramon, & Brass, 2008; Marsh, Mullett, Ropar, & Hamilton, 2014), but de Lange and colleagues (2008) found that unusual actions produced greater response in mirror areas. Note however that even in that study, when participants were asked to judge intentions, greater response was found in mentalizing areas; and even actions which are not implausible tend to produce responses in mentalizing, as well as mirror, areas when participants are asked to judge intentions (Becchio et al., 2012; Ciaramidaro, Becchio, Colle, Bara, & Walter, 2014). Lieberman and colleagues suggest that mirror areas are involved in perceiving *what* is being done, and the way in which an action is performed (action perception; see section 3.2), whereas mentalizing areas are involved when inferring *why* an action is being performed (intention understanding; Spunt et al., 2010, 2011; Spunt & Lieberman, 2012). This suggestion is consistent with van Overwalle and Baetens (2009)'s review which concluded that the mirror system is not involved in mentalizing in general, when biological motion is not present. Thus it appears that mirror areas respond to actions (and may respond more when actions are unusual), but this response may be solely due to the presence of action stimuli: that is, it may be entirely unrelated to the task of identifying the actor's intentions.

Therefore, the extent to which lower-level mirror versus higher-level mentalizing networks are involved in intention understanding appears to depend on the type of stimuli used, and the task instructions (i.e. whether participants have been asked to identify intentions). However, brain imaging measures cannot demonstrate the causal role of brain areas in a particular process; thus sections 3.6 and 3.7 review the causal evidence for the involvement of mirror and mentalizing areas in intention understanding.

3.6. The role of mirror neurons in action perception and intention understanding

Various studies have investigated the causal role of mirror neurons in action *perception*. Data from both neuropsychological lesion studies (see Urgesi, Candidi, & Avenanti, 2014, for a recent meta-analysis) and 'virtual lesion' brain stimulation studies (summarised in Catmur, 2014) indicate that mirror neuron brain areas – in particular, premotor cortex – are required for tasks involving the perception of others' actions. However, few if any of these studies use tasks involving intention understanding.

The study which comes closest to doing so asked participants to judge whether an actor was trying to deceive them by lifting a heavy box as though it were light, and vice-versa (Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013). The authors found that disruptive premotor stimulation impaired participants' ability to judge deception from observed actions; however, they suggest that this effect relates to the fact that good performance in this task relies strongly on processing of kinematic differences between valid and deceptive actions. Thus premotor cortex may contribute to intention understanding via its role in action perception; but these data do not demonstrate a clear role for mirror neuron areas in intention understanding according to the distinction set out in section 3.2.

An elegantly designed study by Michael and colleagues (2014) was the first to address this issue. Participants performed three tasks during disruptive stimulation of premotor cortex. One task tested only action perception; the second tested both action perception and the ability to identify the actor's immediate intention; and the third tested action perception, the ability to identify the actor's immediate intention, and the ability to identify the actor's higher-level intention. If mirror neuron areas are involved in action perception, then disruption of premotor cortex should impair performance on all three tasks. If they are additionally involved in intention understanding, then disruption of premotor cortex should have increased the impairment for the second and third tasks. Crucially, disruptive stimulation of premotor cortex impaired participants' performance on all three tasks, with no significant differences between tasks. As the psychological process common to each task is that of action perception, these data support the claim that mirror neuron areas are involved in action *perception* (which of course may be an initial stage in the identification of others' intentions), but these data do not provide any evidence for the involvement of mirror neuron areas in higher-level processes of intention understanding beyond this initial stage.

3.7. The role of mentalizing areas in intention understanding

Surprisingly few studies have investigated the causal role of mentalizing areas in the ability to infer intentions from actions. This is likely due to two factors: research into mentalizing has focused on other aspects of mentalizing such as theory of mind; and a key node of the mentalizing network, the medial prefrontal cortex, is not easily accessible to brain stimulation techniques. The one study that has investigated the involvement of the mentalizing network in understanding intentions from others' actions targeted the posterior superior temporal sulcus (Stolk et al., 2014). These authors showed that disruptive stimulation of this area impaired the ability to infer intentions from actions in a communicative task. It is clear, however, that further research needs to be performed to establish whether mentalizing areas are required to infer intentions from observed actions.

4. Summary and conclusions

Actions performed with different intentions produce different kinematic profiles, meaning that it is in principle possible to use perceptual information as a starting point for decoding another's intentions; and in most cases observers seem to be able to achieve this, raising the question of whether they do so using direct perceptual or inferential processes. I proposed that four conditions should be fulfilled in order to conclude that others' intentions can be understood using direct perception; the extant data only support two of these conditions. Furthermore, a working definition of the distinction between action perception and intention understanding is required in order to make further empirical progress.

I reviewed three sources of evidence which could contribute data to the question of whether direct or inferential processes underlie intention understanding. Timecourse data do not support the presence of a fast, direct route for intention understanding. Some data suggest that action perception may occur pre-attentively, but there is no evidence that intention understanding does. Brain imaging data suggest that both mirror neuron and mentalizing networks are involved in intention understanding, but there is limited *causal* evidence for the role of either mirror or mentalizing areas in intention understanding. From the existing evidence, it appears that mirror neuron areas are involved in action perception, a process which may be necessary but not sufficient for intention understanding.

Although the evidence is still incomplete, it does not support a direct perception account, and in particular does not support the intention understanding theory of mirror neuron function. Given the current data, the most likely scenario is that mirror areas provide sensorimotor information to mentalizing areas in order to support and constrain inferential processes of intention understanding; future research should focus on testing the causal role of mentalizing areas in acquiring intentions from others' actions in order to support or refute this model.

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